Hunting of Sumatran orang-utans and its importance in determining distribution and density

Wich, S A ; Fredriksson, G M ; Usher, G ; Peters, H H ; Priatna, D ; Basalamah, F ; Susanto, W ; Kühl, H

Abstract: To conserve species it is essential to understand which factors determine their distribution and density. Here we focus on the critically endangered Sumatran orang-utan and examine factors that influence the distribution and density in the Batang Toru area, the southernmost area where wild orang-utans occur on Sumatra. We contrast a scenario in which orang-utan distribution is mainly determined by ecological, and topographic variables with a model that includes hunting and human impact. We show that orang-utan distribution and density are best explained by hunting pressure and elevation. These results indicate that an assessment of anthropogenic factors that might influence density such as hunting needs to be included in surveys that aim to predict orang-utan distribution and density. As anthropogenic impact becomes higher with increasing human population density and increased forest access in most areas where orang-utans occur the consequence is that orang-utan conservation will have to be achieved in an environment modified by humans. In such areas the potential for a range of conflicts such as hunting that lead to human-caused mortality for orang-utans will remain a constant threat and need to be mitigated.

DOI: https://doi.org/10.1016/j.biocon.2011.12.006

Hunting of Sumatran orang-utans and its importance in determining distribution and density

S. A. Wich[1,2], G. M. Fredriksson[1,3], G. Usher[1], H. H. Peters[1], D. Priatna[4], F. Basalamah[5], W. Susanto[5], and H. Kühl[6].

[1] Sumatran Orangutan Conservation Programme (PanEco-YEL), Medan, Sumatra, Indonesia

[2] Anthropological Institute, University of Zurich, Zürich, Switzerland

[3] Institute for Biodiversity and Ecosystem Dynamics / Zoological Museum, University of Amsterdam, Amsterdam, the Netherlands

[4]The Zoological Society of London (ZSL) Indonesia Programme, Bogor, Indonesia

[5]Biology Faculty - Universitas Nasional, Jakarta, Indonesia

[6]Max-Planck-Institute for Evolutionary Anthropology, Department of Primatology, Leipzig, Germany

Corresponding author:
Serge Wich
Sumatran Orangutan Conservation Programme (PanEco-YEL)
Jl. K.H. Wahid Hasyim No 51/74 Medan Baru
Medan 20154 North Sumatra Indonesia
Email: sergewich1@yahoo.com
Tel: +62-61-4514360
Fax: +62-61-4514749

Abstract

To conserve species it is essential to understand which factors determine their distribution and density. Here we focus on the critically endangered Sumatran orang-utan and examine factors that influence the distribution and density in the Batang Toru area, the southernmost area where wild orang-utans occur on Sumatra. We contrast a scenario in which orang-utan distribution is mainly determined by ecological, and topographic variables with a model that includes hunting and human impact. We show that orang-utan distribution and density are best explained by hunting pressure and elevation. These results indicate that an assessment of anthropogenic factors that might influence density such as hunting needs to be included in surveys that aim to predict orang-utan distribution and density. As anthropogenic impact becomes higher with increasing human population density and increased forest access in most areas where orang-utans occur the consequence is that orang-utan conservation will have to be achieved in an environment modified by humans. In such areas the potential for a range of conflicts such as hunting that lead to human-caused mortality for orang-utans will remain a constant threat and need to be mitigated.

Keywords: great ape, Indonesia, spatial model, human dominated landscape

1. Introduction

Effective species conservation requires solid understanding of the factors that determine the distribution and density of the species. As a result there is a large body of literature from studies that have examined factors that influence the distribution (Elith et al. 2006; Guisan and Thuiller 2005) and density of species (Eltz et al. 2002; Karanth et al. 2004). These studies have shown that ecological factors such as vegetation type (Karanth and Sunquist 1992; Peres 1997), fruit-tree density (Balcomb et al. 2000; Marshall et al. 2009a; van Schaik et al. 1995; Wich et al. 2004)), altitude (Bruhl et al. 1999; Heaney et al. 1989; Lammertink 2004; van Schaik et al. 1995), climate (Hill 1999), and prey-density (Karanth et al. 2004) have an influence on species' distribution and density. Although these factors are important in conditions where human influence is limited, many species find themselves in human dominated landscapes where anthropogenic factors have an

impact on species' distribution and density, which can be even more important. Such factors are habitat alteration through logging or other means (Chapman et al. 2000; Eltz et al. 2002; Felton et al. 2003; Hill et al. 1995; Meijaard et al. 2005) ; habitat fragmentation (Henle et al. 2004; Kattan et al. 1994; Laurance 1990; Şekercioglu et al. 2002; Turner 1996) ; disease (Koendgen et al. 2008; Walsh et al. 2003; Walsh et al. 2005); and hunting (Altrichter and Boaglio 2004; Kühl et al. 2009; Marshall et al. 2006; Meijaard et al. 2010b; Peres 1997; Reinartz et al. 2006; Rijksen and Meijaard 1999). It is therefore clear that focusing purely on ecological factors in models for distribution and density will not be sufficient.

Here we focus on the Sumatran orang-utan (*Pongo abelii*), a critically endangered orang-utan species that only occurs on the Indonesian island of Sumatra and for which a conservative estimate of 6,600 individuals in the wild is given (Wich et al. 2008). Our main aim is to evaluate which factors determine their distribution and density in a human dominated landscape. Although there have been several attempts to determine the factors that influence the distribution and density of Sumatran orang-utans (Husson et al. 2009; van Schaik et al. 1995; Wich et al. 2004), there has been only one study that examined the influence of hunting and other ecological variables on orang-utan density in a multivariate approach (Marshall et al. 2006). The Marshall et al. (2006) study was conducted for Borneo and so far no studies for Sumatran orang-utans exist. Such data are important for two main reasons. First, because the authorities are not adequately addressing the hunting issues data on the effects of hunting can be used to convince the appropriate authorities to start dealing with the hunting issue (Rijksen and Meijaard 1999). Second, to start monitoring the long-term impact of hunting on orang-utan populations, which so far only comes from population viability models without any monitoring data to test the accuracy of such models (Marshall et al. 2009b). There are no data available indicating that disease might have influenced orang-utan distribution or density so we do not address this factor here while acknowledging that more work on this aspect needs to be done. Although at present we cannot yet make models for the whole potential orang-utan distribution on Sumatra, we have a relatively large dataset available for one of the populations namely the Batang Toru population (Wich et al. 2008; Wich et al. 2003), for which also information on hunting pressure also exists from a recent

questionnaire (Usher, pers.com.). This allows us to examine the relative contributions of hunting pressure, ecological, topographic and climate factors on orang-utan distribution and density.

Hunting has been shown to influence orang-utan density (Marshall et al. 2006) and might have been responsible for lower orang-utan densities at present than compared to the past (Meijaard et al. 2010b). It has also been suggested that hunting could be related to gaps in orang-utan distribution on Sumatra and Borneo (Rijksen and Meijaard 1999) and that a very modest hunting pressure can send a population into an extinction trajectory (Marshall et al. 2009b). However, there have been no studies using actual hunting pressure data in a predictive model in combination with other factors that are known to influence orang-utan distribution and density to investigate the importance of hunting in relation to these other factors. Identifying the importance of the various factors is important since it can help determine whether conservation action needs to address hunting and human impact or whether the impact of these is so low that the effects on density and distribution are negligible and that conservation efforts can therefore better be applied elsewhere. The main other factors that have been examined for their influence on orang-utan density are forest integrity and topographic parameters (Husson et al. 2009; Wich et al. 2004), but in those studies hunting pressure was not included. Our approach here therefore represents the first attempt to model orang-utan distribution and density while incorporating the main factors that have been argued to influence these.

2. Methods

2.1 Field methods

2.1.1 Study area

The Batang Toru forest area is located just southwest of the large lake Toba in the province of North Sumatra. The area can be divided in a western and eastern forest block that are separated by the Batang Toru river and a large fertile valley which has been farmed for several centuries (Fig. 1). The forests in this area range from 150 m to 1800 m elevation, with some 75% of the forest being above 750 m. The forest area where orang-utans are thought to occur is 1093 km2 in total (844 km2 west and 249 km2 east). The forests can mostly be characterized as lower montane, with the most common tree

families being Sapotaceae, Myrtaceae and Lauraceae. Most of the terrain is extremely rugged and a large proportion of the area has slopes of 40% or greater.

The Batang Toru area contains the southernmost known orang-utan population on Sumatra and orang-utans were rediscovered here in 1997 (Meijaard 1997). This orang-utan population was thought to be isolated from the more northern populations in Sumatra because of large gaps in forest cover between the areas (Wich et al. 2003). Subsequent research in the area indicated that the population's mitochondrial DNA is very different from the orang-utans occurring in the more northern parts of Sumatra and more closely clustered with Bornean orang-utans, indicating the uniqueness of this population (Nater et al. 2011). Its uniqueness also comes from being the only orang-utan population in a dryland forest where tool-use on *Neesia* sp. fruits has been observed in a small upland peatswamp, which previously has only been reported for orang-utans in coastal peatswamp forests (van Schaik 2009). Wich et al. (2008) estimated the orang-utan population for the area to be 550, with 400 for the western and 150 individuals for the eastern forest block (Fig. 1).

2.1.2 Field data collection

We conducted a total of 72 line transects of varying length in the area between 2003 and 2009. These were unrelated surveys and not part of an overall design. We used standard methods to detect nests (Buij et al. 2003; Schaik van et al. 1995; van Schaik et al. 1995). All observers were well trained and the methodology was consistent between observers Along each transect a minimum of three observers slowly walked the transect and carefully looked for nests. For each observed nest the perpendicular distance was measured with a tape measure or on occasions that the terrain did not allow for tape measurements, the distance was measured with a rangefinder. For each nest observed the perpendicular distance in meters was measured with a measuring tape, the height of the nest was estimated in 5-meter interval classes, and the decay stage of the nest was recorded. Nest decay was measured in a four-class system: (A) fresh, some leaves still green; (B) nest is brown but remains intact; (C) leaves missing and holes appearing in nest; (D) leaves are gone, only branch structure of nest remains.

149 Information on hunting was obtained from the Sumatran Orangutan Conservation
150 Programme who conducted 4 socio-economic surveys covering 4 separate geographical
151 areas around the Batang Toru forests between October 2007 and February 2009. A total
152 of 2,811 respondents in 378 locations, representing 2.12% of the total population living
153 around the forests, were interviewed using a questionnaires consisting of up to 174
154 questions. Respondents were mainly adult males. Question 100 asked "which species are
155 often hunted or obtained?", with check boxes for over 20 species plus an option for
156 adding further species. Data from the 4 surveys were collated into a unified database, and
157 an additional field added for the spatial location of the respondent. The database was
158 analyzed using SurveyPro 3.0, and orangutan hunting data exported to a spreadsheet file
159 which was then linked to the attribute table of a GIS point shapefile to allow for visual
160 representation of the distribution of orangutan hunters as a proportion of the total number
161 of respondents at each location.
162
163 ***2.2 Analytical methods***
164
165 *2.2.1. Covariates*
166 To explain variation in orang-utan density as a function of hunting pressure and other
167 environmental variables and to build a predictive spatial model, we identified several
168 covariate datasets, each belonging to one of the categories topography (altitude, slope),
169 ecological/habitat condition (forest type, above ground carbon), human impact (% orang-
170 utan hunters in neighbouring villages, distance to forest edge) and climate (average
171 annual rainfall, variation in annual rainfall). We extracted the mean value of all
172 covariates, except 'distance to forest edge' in a neighbourhood of half the transect length
173 around each transect midpoint, and also for 1x1km sized grid cells, covering the survey
174 area, which we needed to make spatial predictions. 'Distance to forest edge' we extracted
175 as the value of the location of the transect midpoint and of the grid cell centerpoint (*see*
176 *supplementary information for details on the various layers*). We did not consider
177 geographic barriers in those calculations.
178

We conducted correlation, principal component (PCA) and factor analyses (FA) to evaluate the degree of multicollinearity between the different covariates and to potentially reduce the number of predictors. Whereas some variables were highly correlated (topographic and climate variables, vegetation variables), PCA and FA did not provide a considerable reduction in the number of predictor variables that we considered useful. We therefore decided to select only those covariates that correlated less than 0.5 with any other predictor variable. Thus we ended up with the topographic variables 'altitude', 'slope', the human impact variables 'distance of transect to forest edge', 'percentage of orang-utan hunters in villages' and the ecological/habitat condition variable 'proportion primary forest'. We did not include any climate variables, since they were well represented by the topographic variables (*supplementary information*, Table S2).

Furthermore, we developed an autocorrelation term as additional predictor (*see supplementary information*). Environmental, ecological and human covariates usually explain only a certain proportion of observed density variation. A much larger proportion of the variance remains usually unexplained and parts of it can often be attributed to 'spatial autocorrelation' between sampling locations (Dormann et al. 2007; Lichstein et al. 2002). All covariates and the autocorrelation term were z-transformed for facilitating model parameter comparison.

2.2.2. Modelling

For analyzing the combined influence of the five covariates and in particular for assessing the impact of hunting on orang-utan density and to build a predictive orang-utan density model for the survey area, we used Generalized Linear Modeling (GLM) (McCullagh and Nelder 1989). In order to build an appropriate model, we had to consider several issues. First, orang-utan transect nest count data are usually skewed with a high proportion of transects with only few observations and few transects with a large number of nest observations. To account for this, we included a negative binomial error function. Second, our data were collected along transects of differing length. We accounted for this by including an offset term into our model that relates the density prediction of the model to the area covered by transects of differing length (Hedley and Buckland 2004). Third, to

account for spatially autocorrelated residuals, we included an autocorrelation term as additional predictor into the model (*see supplementary information*). Fourth, we expected 'altitude' and 'hunting' to influence orang-utan density in a nonlinear way. Therefore, we included for both predictor variables also squared terms into the model, as well as an interaction term between altitude and hunting. Thus our full model became

orang-utan nest density ~ altitude + slope + proportion primary forest + hunting + distance to forest edge + altitude² + hunting² +altitude*hunting + autocorrelation + offset + error term

To evaluate the combined influence of the five covariates and in particular the effect of hunting, we ran the full model and compared it with the reduced model not containing the hunting effect. For reasons of model uncertainty in spatial model prediction, we also evaluated all possible combination of models (n=104), for which we derived AIC and AIC weights.

To evaluate whether modelling assumptions were met and to evaluate the goodness of fit of the developed models we ran a series of model diagnostics including the assessment of residuals, observed vs. predicted values, Cook' distance, DFbeta, DFfits and QQ-plots (*see supplementary information*). All analyses were conducted using R (version 2.9.1, R Development Core Team, 2005).

2.2.3. Nest decay and estimation of orang-utan density

For converting orang-utan nest density into orang-utan density, the former need to be divided by nest decay time, daily nest construction rate and the proportion of nest builders (Kühl et al. 2008; van Schaik et al. 1995). Daily nest construction rate and proportion of nest builders can only be estimated following habituated individuals. We therefore took values for these two variables from the literature (see below under prediction heading for details). For estimating nest decay time, we had a data set on 386 freshly built nests from Batang Toru available. Each nest was revisited one to 10 times after it was built. For each nest, we extracted the date of first visit that approximated construction and the day of the last visit, no matter, whether the nest had decayed or not.

241 We then ran a logistic regression with normalized intercept (Laing et al. 2003) and
242 included age of the nest as the only predictor. We estimated mean decay time by
243 summing the product of daily decay probability and time elapsed since construction over
244 2000 days (*supplementary information*).
245
246 *2.2.4. Prediction*
247 Because the BT survey area was not defined prior to the transect sampling, we limited
248 spatial predictions to an area of 5km around each transect midpoint, with a total surface
249 of 973km². This we justified by information about the scale of orang-utan ranging
250 behaviour (Singleton et al. 2009). To derive model predictions of orang-utan density and
251 abundance for this area, we generated a 1x1km grid to which we assigned values of the
252 five covariates and the autocorrelation term. The autocorrelation term, we interpolated
253 non-parametrically from the values calculated for each transect (*see supplementary*
254 *information*). We then generated AIC weighted nest density model predictions with each
255 of the 104 models and summed the predictions for each cell. We then divided the nest
256 density value for each cell mean by the estimated mean nest decay time, a nest
257 construction rate of 1.7 days (Buij et al. 2003) and a proportion of nest builders of 0.9
258 (Buij et al. 2003) to derive orang-utan density estimates per cell. The sum of all cell
259 values gave the estimated orang-utan abundance. We used parametric bootstrap repeated
260 1000 times to derive 95% confidence limits (*see supplementary material*).
261
262 **3. Results**
263 *3.1. General*
264 In total 602 orang-utan nests were encountered on the 72 transects (111.8 km total length)
265 sampled in the BT area. Mean nest encounter rate per km was 5.38 ± 8.7 (SD) and ranged
266 from 0-33.7 nests per km.
267
268 *3.2. Covariate modelling*
269 Orang-utan nest density was much better predicted by the full model including all five
270 covariates and the autocorrelation term than by the reduced model without the hunting
271 information (likelihood ratio test 11.51; Df=2; $p<0.01$) (Table 1). This result was also

supported by the fact that all models in the 95% confidence set contained the hunting information variable and interaction between hunting and altitude (Table S1). The interaction between hunting and altitude is complex (Fig. 2). At low altitude, hunting pressure has a negligible effect on orang-utan density, because OU density is low in general, but at higher altitude an increase in hunting pressure is related to a considerable increase in orang-utan density (Fig. 2). Furthermore, nest density showed a positive quadratic relationship with altitude with a maximum between 500-800m (Fig. 3; Table1). Also, the autocorrelation term was highly significant indicating the strong spatial correlation of nest density (Fig. 3f). The 'proportion of primary forest' and 'distance to forest edge' were the least important predictors (Table 1; Fig. 3).

3.3. Nest decay

We estimated mean nest decay time at 503 days with a 95% confidence limits of 458-548 days and a coefficient of variation of 0.045. The fit of the logistic decay model was very good (χ^2, $p<0.001$) (Fig. 4).

3.4. Spatial prediction, orang-utan distribution, density and abundance estimates

The model prediction of orang-utan density for the survey area provided estimates varying from zero to almost seven orang-utans per km² with a cluster of higher density occurring in the west of Batang Toru (Fig.1). Mean orang-utan density in the survey area was 0.23 individuals/km². Total orang-utan abundance for the survey area of 973 km² was estimated to be 225 (95% CI 147-363) individuals with 74 (95% CI 45-112) in the East (585km²) and 151 (95% CI 94-231) (388km²) in the western part.

4. Discussion

In this paper we contrast models for orang-utan distribution and density containing only ecological and topographic factors with models in which hunting and human impact are incorporated. Although several previous studies have addressed the effect of such factors on orang-utan density separately or in multivariate models (Felton et al. 2003; Husson et al. 2009; Marshall et al. 2006; Meijaard et al. 2010b; van Schaik et al. 1995; Wich et al. 2004), this is the first study to use a predictive model to assess this. These studies have

shown that several ecological and topographic factors can influence orang-utan density in remaining habitat, but that orang-utan density is predominantly influenced by anthropogenic factors such as logging and hunting. Although both negatively affect orang-utan density in general, in Borneo logging appears to have less of an effect on orang-utan density than on Sumatra (Ancrenaz et al. 2010; Husson et al. 2009) and orang-utans on Borneo showing some resilience in human altered landscape mosaics (Meijaard et al. 2010a). We have examined nest density here for a high-altitude orang-utan population compared to other studies and expectedly nest decay rates are higher than what has been previously documented for Sumatra (Husson et al. 2009) and close to some of the rates reported for East Kalimantan (Mathewson et al. 2008)

The results of our analyses show that orang-utan hunting and altitude are the two most important factors explaining orang-utan density for the Batang Toru area, but in a somewhat non-intuitive way. Where the questionnaires (Usher, pers. com) indicate high orang-utan hunting pressure one would perhaps expect low orang-utan density, but our result show the opposite pattern. Where orang-utan hunting reports are high, orang-utan density is high and this effect is strongest at an intermediate altitude. At low altitude orang-utan density is low, perhaps due to previous hunting in these areas where access is relatively easy. This could have resulted in a currently low hunting incidence since orang-utans are hardly present in those areas anymore. At high altitude there are ecological constraints on orang-utan density such as fruit productivity that cause a low density (Djojosudharmo and van Schaik 1992). As a result the effect of hunting is most pronounced at intermediate altitude since that is where orang-utan density is highest.

The perhaps surprisingly positive relationship between hunting and orang-utan density indicates that hunting predominantly is reported from areas where orang-utan density is still relatively high and orang-utans are therefore presumably easier to find and hunt. This result indicates that one needs to design questionnaires carefully to be able to make inferences about orang-utan density from hunting interview data. At least some questions would need to address whether orang-utans were observed while being in the forest and not hunting (Meijaard et al. 2011).

As expected distance from forest edge (0-5.13km) was positively related to orang-utan density. This can be explained by the fact that further away from the forest edge

334 hunting pressure is also expected to be lower because the questionnaire data show that on
335 76% of the trips people make to the forest these trips are less than a day long, which
336 limits the distance they can cover in the forest. These findings are similar to the one other
337 study that has investigated orang-utan density and distance from the forest edge (Marshall
338 et al. 2006).
339 The results here also indicate that at present it is becoming increasingly difficult
340 to determine which non-anthropogenic factors are important in determining orang-utan
341 density because hunting has an influence on orang-utan density. It is possible that
342 previous hunting has lowered orang-utan density in areas where hunting is not reported
343 from and that orang-utan density is below carrying capacity in such areas and will fall
344 below carrying capacity in all areas if hunting continues. Although at present we cannot
345 show this, a study that was conducted on Borneo indicated that overall hunting might
346 have lowered densities on the island (Meijaard et al. 2010b). It would be very interesting
347 to determine whether the Batang Toru orang-utan population is in a downward trend or
348 not, but unfortunately no life history nor specific hunting data on age-sex distribution of
349 hunted orang-utans are available at present to assess this. However, modelling has
350 indicated that even very low levels of hunting on females could send a population
351 towards extinction (Marshall et al. 2009b) and it is therefore a strong possibility that the
352 orang-utan population in Batang Toru is in such a downward trend.
353 To establish which non-anthropogenic factors are important in determining
354 Sumatra orang-utan density one therefore needs to study the orang-utans in the Leuser
355 Ecosystem (a large conservation area north of the Toba lake) where hunting orang-utans
356 for food has been absent for religious reasons for a long-time (Rijksen and Meijaard
357 1999) and previous studies have found correlations between ecological and topographical
358 features and orang-utan density in the remaining primary rainforests (van Schaik et al.
359 1995; Wich et al. 2004). This problem is also profound for African great apes which are
360 hunted extensively and intensively (Fa and Brown 2009; Kühl et al. 2009; Remis and
361 Kpanou 2011).
362 Since human dominated landscapes are becoming the norm for areas in which
363 orang-utans occur it is important to determine how we can effectively conserve orang-
364 utans in such landscapes. From this and other studies it is clear that logging and hunting

are the main negative factors (Husson et al. 2009; Marshall et al. 2009b; Marshall et al. 2006; Rijksen and Meijaard 1999). Although logging of forests where orang-utans occur generally has a negative impact (Husson et al. 2009), its impact can be mitigated to some extent by reduced impact logging (Ancrenaz et al. 2010; Marshall et al. 2006) and leaving the forest to recover after logging (Knop et al. 2004). Hunting has been long suspected to be the main factor for disappearance of orang-utans from large parts of their former range (Rijksen and Meijaard 1999). The only previous field study on hunting shows clearly that hunting has a negative impact on orang-utan population density (Marshall et al. 2006) and modelling studies indicate that low levels of hunting can set an orang-utan population on a path to extinction (Marshall et al. 2009b). Studies on hunting are therefore important to determine that hunting indeed occurs and to examine how large the negative effect of hunting on population density is. As has been suggested many times before, an important aspect of mitigating the hunting threat is to increase the effectiveness of law enforcement (Rijksen and Meijaard 1999). Killing of orang-utans has been illegal under Indonesian law for more than 80 years, but enforcing this law by prosecuting the people involved in orang-utan hunting has to the best of our knowledge never occurred. While an increase in law enforcement is important there should also be strong awareness campaigns and education efforts to explain people that hunting of orang-utans is not only illegal, but also simply 'not done' in a modern society. As long as hunting of orang-utans occurs the survival of orang-utans in human dominated landscapes is unlikely.

Acknowledgements

We thank Ned Horning for the R-script forest classification and Alessandro Baccini for providing the above ground carbon layer. The authors thank BOS Netherlands, Great Ape Trust of Iowa, the Durrell Wildlife Conservation Trust and Ouwehands Zoo Foundation for financial support. Yayasan Ekosistem Lestari and PanEco are also thanked for their support of the project.

395

Table 1: Covariate modeling results for the best model with lowest AIC, the full model, the model with no hunting effect and the null model. Listed is the number of parameters, AIC, AIC weight, the parameter estimates for the coefficients.

Model	**par**	**AIC**	**AICw**	**int**	**alt**	**alt²**	**slope**	**hunt**	**hunt²**	**dist.for**	**forest**	**alt:hunt**	**ac**
alt+alt²+hunt+alt:hunt+ac	6	403	0.2	1.95	10.05	-37.34	-	0.2	-	-	-	3.14	0.11
alt+alt²+slope+hunt+hunt² +dist.forest+forest+alt:hunt+ac	10	409	0.0	1.87	9.51	-37.29	0.02	1.25	-1.12	0.06	0.26	3.23	0.12
alt+alt²+slope+dist.forest+forest+ac	7	415	0.0	2.87	4.63	-27.25	0.01	-	-	0.36	0.45	-	0.1
alt+alt²+slope+forest+ac	6	416	0.0	2,65	4.79	-28.79	1.4E-04	-	-	-	0.72	-	0.1
ac	2	434	0.0	4.93	-	-	-	-	-	-	-	-	0.17
p-values				**<0.01**	**<0.01**	**<0.01**	**0.24**	**0.23**	**0.08**	**0.23**	**0.1**	**<0.01**	**<0.01**

Figure legends

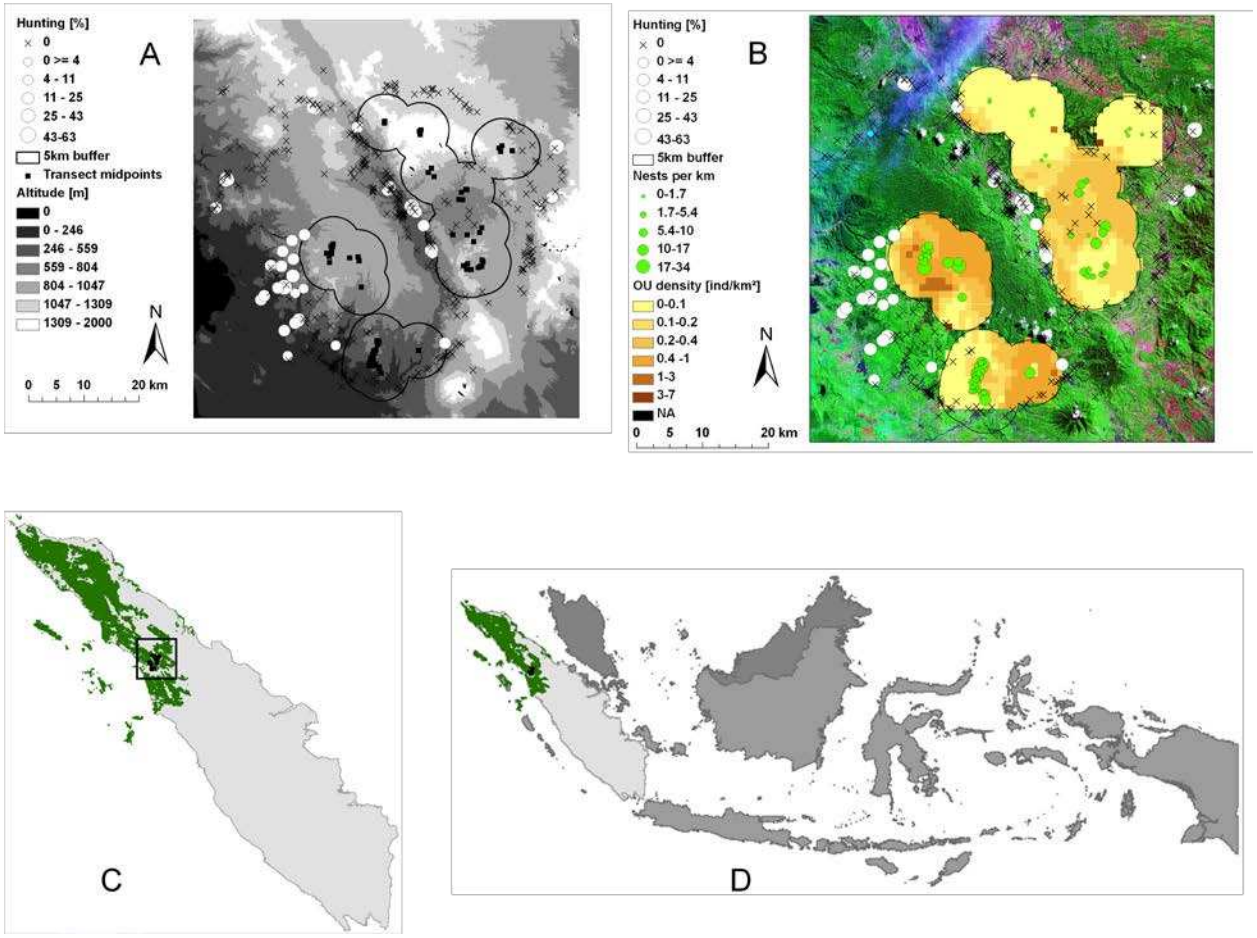
Fig. 1: Maps of Batang Toru study area showing altitude, location of transects and hunting information (A) and orang-utan density surface (B); (C) Location of Batang Toru study area within Sumatra, in green forest cover for Aceh and North Sumatra provinces; and (D) Location of Sumatra within Indonesia. Hunting is presented as the percentage of interviewed villagers in each village that stated they hunted orang-utans. The crosses (x) and circles indicate the location of the villages.

Fig. 2: Perspective plot of orang-utan density as a function of altitude+altitude^2+hunting+altitude*hunting+autocorrelation

Fig. 3: Scatter plots of (a) altitude, (b) slope, (c) hunting, (d) distance to forest, (e) proportion primary forest vs. nest encounter rate and (f) the autocorrelation values at neighboring transect locations vs. model residuals

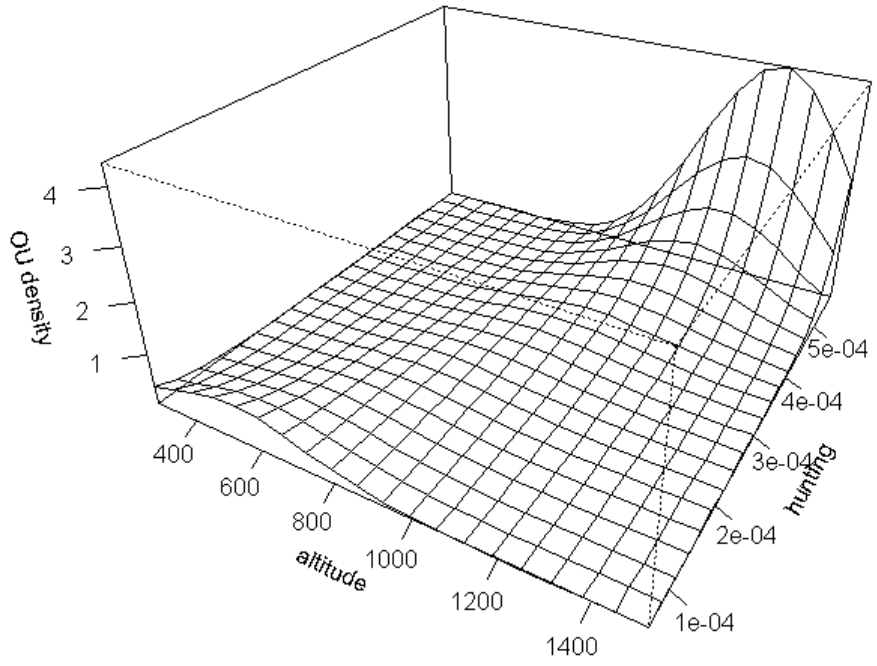
Fig. 4: Time series of the proportion of surviving nests from the study site (open circles) and nest decay model prediction (solid line).

438 Fig. 1


Hunting [%]
0
0 >= 4
4 - 11
11 - 25
25 - 43
43-63
5km buffer
Transect midpoints
Altitude [m]
0
0 - 246
246 - 559
559 - 804
804 - 1047
1047 - 1309
1309 - 2000
A
N
0 5 10 20 km
Hunting [%]
0
0 >= 4
4 - 11
11 - 25
25 - 43
43-63
5km buffer
Nests per km
0-1.7
1.7-5.4
5.4-10
10-17
17-34
OU density [ind/km²]
0-0.1
0.1-0.2
0.2-0.4
0.4 -1
1-3
3-7
NA
B
N
0 5 10 20 km
C
D

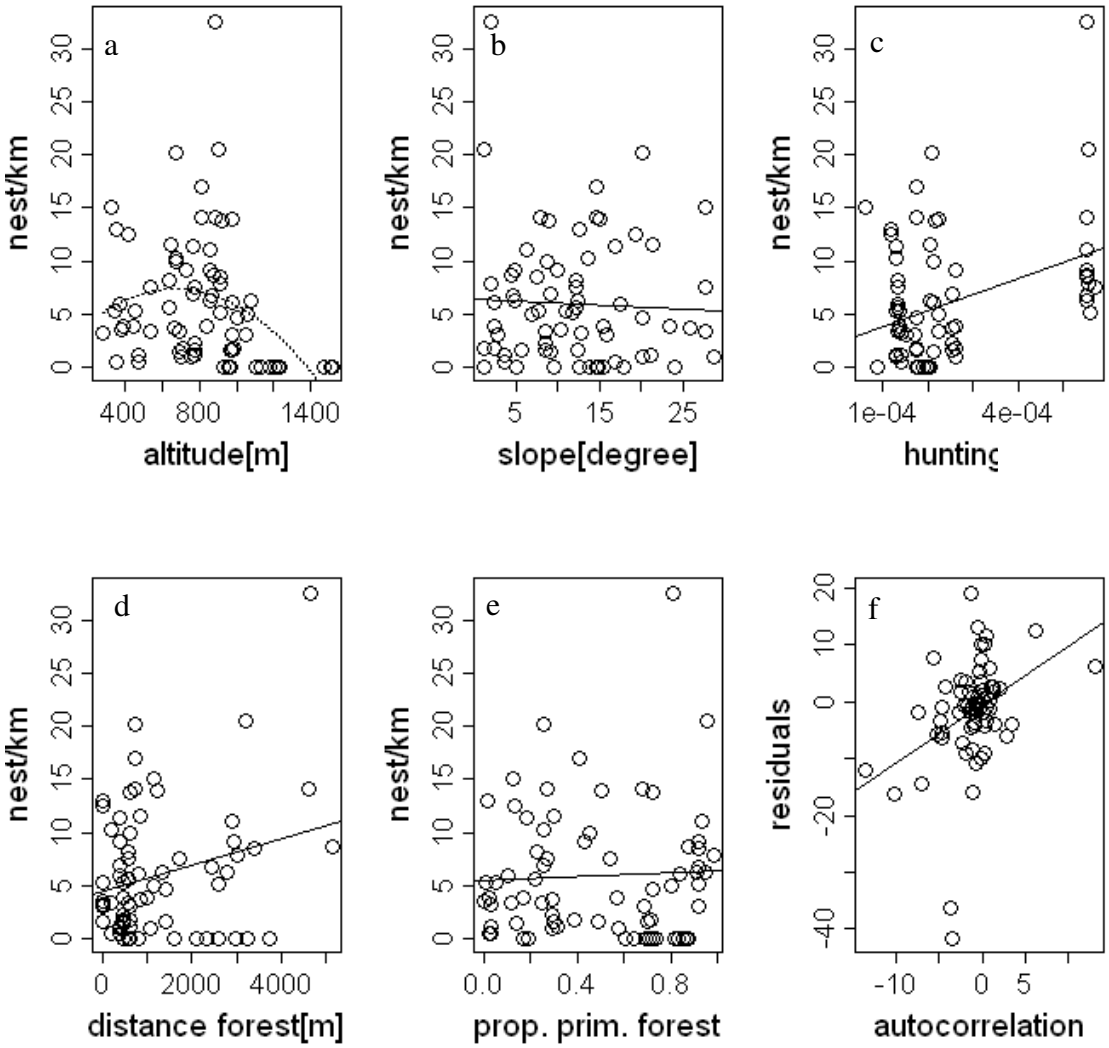
439

440 Fig. 2


OU density
4
3
2
1
altitude
400
600
800
1000
1200
1400
hunting
1e-04
2e-04
3e-04
4e-04
5e-04

441

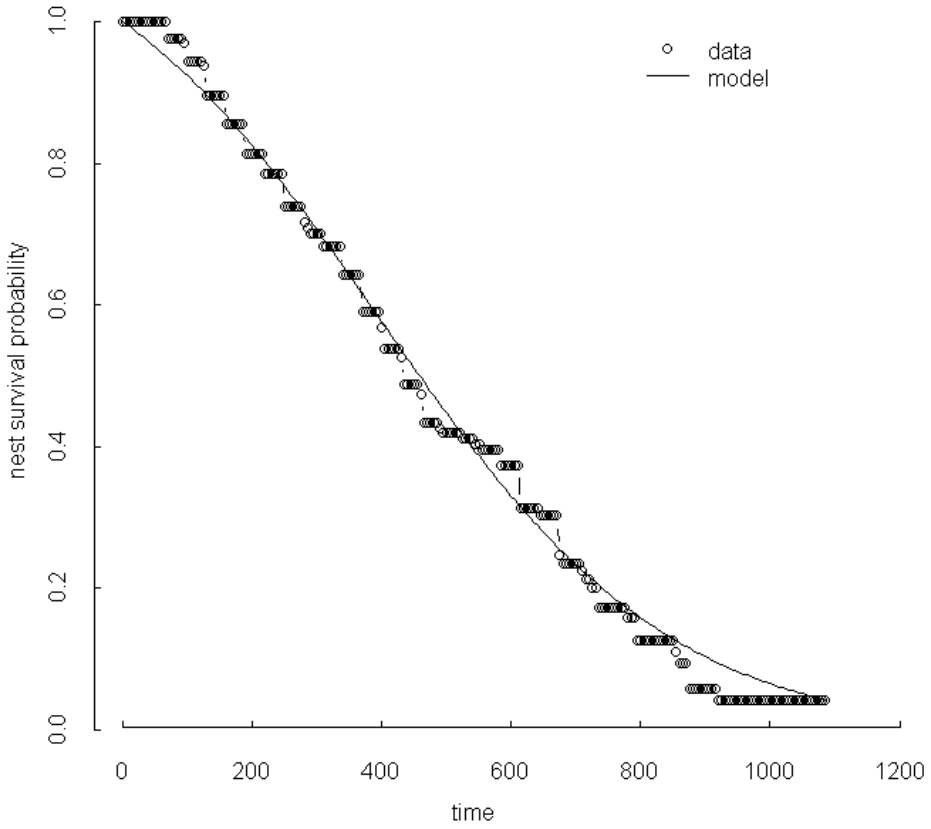
442 Fig. 3



443

444

445 Fig. 4



446
447
448
449
450
451
452
453
454
455
456
457
458
459

460 References

461 Altrichter, M., Boaglio, G.I., 2004. Distribution and relative abundance of peccaries in
462 the Argentine Chaco: associations with human factors. Biological Conservation 116,
463 217-225.
464 Ancrenaz, M., Ambu, L., Sunjoto, I., Ahmad, E., Manokaran, K., Meijaard, E., Lackman,
465 I., 2010. Recent surveys in the forests of Ulu Segama Malua, Sabah, Malaysia, show
466 that orang-utans (*P. p. morio*) can be maintained in slightly logged forests. PLOS
467 ONE 5, e11510.
468 Balcomb, S.R., Chapman, C.A., Wrangham, R.W., 2000. Relationship between
469 chimpanzee (Pan troglodytes) density and large, fleshy-fruit tree density:
470 conservation implications. American Journal of Primatology 51, 197-203.
471 Bruhl, C.A., Mohamed, V., Linsenmair, K.E., 1999. Altitudinal distribution of leaf litter
472 ants along a transect in primary forests on Mount Kinabalu, Sabah, Malaysia. Journal
473 of Tropical Ecology 15, 265-277.
474 Buij, R., Singleton, I., Krakauer, E., Schaik, C.P.v., 2003. Rapid assessment of orangutan
475 density. Biol. Cons. 114, 103-113.
476 Chapman, C.A., Balcomb, S.R., Gillespie, T.R., Skorupa, J.P., Struhsaker, T.T., 2000.
477 Long-term effects of logging on African primate communities: a 28-year comparison
478 from Kibale National Park, Uganda. Conservation Biology 14, 207-217.
479 Djojosudharmo, S., van Schaik, C.P., 1992. Why are orang utans so rare in the highlands?
480 Altitudinal changes in a Sumatran forest. Trop. Biodiv. 1, 11-22.
481 Dormann, C.F., McPherson, J.M., Araujo, M.B., Bivand, R., Bolliger, J., Carl, G.,
482 Davies, R.G., Hirzel, A., Jetz, W., Kissling, W.D., Kühn, I., Ohlemüller, R., Peres-
483 Neto, P.R., Reineking, B., Schröder, B., Schurr, F.M., Wilson, R., 2007. Methods to
484 account for spatial autocorrelation in the analysis of species distributional data: a
485 review. Ecography 30, 609-628.
486 Elith, J., H. Graham, C., P. Anderson, R., Dudík, M., Ferrier, S., Guisan, A., J. Hijmans,
487 R., Huettmann, F., R. Leathwick, J., Lehmann, A., Li, J., G. Lohmann, L., A.
488 Loiselle, B., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., McC. M.
489 Overton, J., Townsend Peterson, A., J. Phillips, S., Richardson, K., Scachetti-Pereira,
490 R., E. Schapire, R., Soberón, J., Williams, S., S. Wisz, M., E. Zimmermann, N.,
491 2006. Novel methods improve prediction of species' distributions from occurrence
492 data. Ecography 29, 129-151.
493 Eltz, T., Bruehl, C.A., van der Kaars, S., Linsenmair, K.E., 2002. Determinants of
494 stingless bee nest density in lowland dipterocarp forests of Sabah, Malaysia.
495 Oecologia 131, 27-34.
496 Fa, J.E., Brown, D., 2009. Impacts of hunting on mammals in African tropical moist
497 forests: a review and synthesis. Mammal Review 39, 231-264.
498 Felton, A.M., Engstrom, L.M., Felton, A., Knott, C.D., 2003. Orangutan population
499 density, forest structure and fruit availability in hand-logged and unlogged peat
500 swamp forests in West Kalimantan, Indonesia. Biological Conservation 114, 91-101.
501 Guisan, A., Thuiller, W., 2005. Predicting species distribution: offering more than simple
502 habitat models. Ecology Letters 8, 993-1009.
503 Heaney, L.R., Heideman, P.D., Rickart, E.A., Utzurrum, R.B., Klompen, J.S.H., 1989.
504 Elevational zonation of mammals in the central Philippines. J. Trop. Ecol. 5, 259-
505 280.

506 Hedley, S.L., Buckland, S.T., 2004. Spatial models for line transect sampling. Journal of
507 Agricultural Biological and Environmental Statistics 9, 181-199.
508 Henle, K., Davies, K.F., Kleyer, M., Margules, C., Settele, J., 2004. Predictors of species
509 sensitivity to fragmentation. Biodiversity and Conservation 13, 207-251.
510 Hill, J.K., 1999. Butterfly spatial distribution and habitat requirements in a tropical forest:
511 impacts of selective logging. Journal of Applied Ecology 36, 564-572.
512 Hill, J.K., Hamer, K.C., Lace, L.A., Banham, W.M.T., 1995. Effects of selective logging
513 on tropical forest butterflies on buru, indonesia. Journal of Applied Ecology 32, 754-
514 760.
515 Husson, S.J., Wich, S.A., Marshall, A.J., Dennis, R.D., Ancrenaz, M., Brassey, R.,
516 Gumal, M., Hearn, A.J., Meijaard, E., Simorangkir, T., Singleton, I., 2009.
517 Orangutan distribution, density, abundance and impacts of disturbance, In
518 Orangutans: Geographic variation in behavioral ecology and conservation. eds S.A.
519 Wich, S.S. Utami Atmoko, T. Mitra Setia, C.P.v. Schaik, pp. 77-96. Oxford Univ
520 Press, New York.
521 Karanth, K.U., Nichols, J.D., Kumar, N.S., Link, W.A., Hines, J.E., 2004. Tigers and
522 their prey: Predicting carnivore densities from prey abundance. Proceedings of the
523 National Academy of Sciences of the United States of America 101, 4854-4858.
524 Karanth, U.K., Sunquist, M.E., 1992. Population structure, density and biomass of large
525 herbivores in the tropical forests of Nagarahole, India. J. Trop. Ecol. 8, 21-35.
526 Kattan, G.H., Alvarez-López, H., Giraldo, M., 1994. Forest fragmentation and bird
527 extinctions: San Antonio eighty years later. Conservation Biology 8, 138-146.
528 Knop, E., Ward, P.I., Wich, S.A., 2004. A comparison of orang-utan density in a logged
529 and unlogged forest on Sumatra. Biological Conservation 120, 187-192.
530 Koendgen, S., Kuehl, H., N'Goran, P.K., Walsh, P.D., Schenk, S., Ernst, N., Biek, R.,
531 Formenty, P., Maetz-Rensing, K., Schweiger, B., Junglen, S., Ellerbrok, H., Nitsche,
532 A., Briese, T., Lipkin, W.I., Pauli, G., Boesch, C., Leendertz, F.H., 2008. Pandemic
533 human viruses cause decline of endangered great apes. Current Biology 18, 260-264.
534 Kühl, H., Maisels, F., Ancrenaz, M., Williamson, E.A., 2008. Best practice guidelines for
535 surveys and monitoring of great ape populations. IUCN, Gland, Switzerland.
536 Kühl, H.S., Nzeingui, C., Yeno, S.L.D., Huijbregts, B., Boesch, C., Walsh, P.D., 2009.
537 Discriminating between village and commercial hunting of apes. Biological
538 Conservation 142(7), 1500-1506.
539 Laing, S.E., Buckland, S.T., Burns, R.W., Lambie, D., Amphlett, A., 2003. Dung and
540 nest surveys: estimating decay rates. Journal of Applied Ecology 40, 1102-1111.
541 Lammertink, M., 2004. A multiple-site comparison of woodpecker communities in
542 bornean lowland and hill forests. Conservation Biology 18, 746-757.
543 Laurance, W.F., 1990. Comparative responses of five arboreal marsupials to tropical
544 forest fragmentation. Journal of Mammalogy 71, 641-653.
545 Lichstein, J.W., Simons, T.R., Shriner, S.A., Franzreb, K.E., 2002. Spatial autocorrelation
546 and autoregressive models in ecology. Ecological Monographs 72, 445-463.
547 Marshall, A.J., Ancrenaz, M., Brearley, F.Q., Fredriksson, G.M., Ghaffar, N., Heydon,
548 M., Husson, S.J., Leighton, M., McConkey, K.R., Morrogh-Bernard, H.C., Proctor,
549 J., Schaik, C.P. van, Yeager, C., Wich, S.A., 2009a. The effects of forest phenology
550 and floristics on populations of Bornean and Sumatran orangutans, In Orangutans:
551 Geographic variation in behavioral ecology and conservation. eds S.A. Wich, S.S.

552 Utami Atmoko, T. Mitra Setia, C.P.van Schaik, pp. 97-118. Oxford University Press,
553 New York.
554 Marshall, A.J., Lacy, R., Ancrenaz, M., Byers, O., Husson, S.J., Leighton, M., Meijaard,
555 E., Rosen, N., Singleton, I., Stephens, S., Traylor-Holzer, K., Utami Atmoko, S.S.,
556 van Schaik, C.P., Wich, S.A., 2009b. Orangutan population biology, life history, and
557 conservation, In Orangutans: Geographic variation in behavioral ecology and
558 conservation. pp. 311-326. Oxford Univ Press, New York.
559 Marshall, A.J., Nardiyono, Engstroem, L.M., Pamnungkas, B., Palapa, J., Meijaard, E.,
560 Stanley, S.A., 2006. The blowgun is mightier than the chainsaw in determining
561 population density of Bornean orangutans (*Pongo pygmaeus morio*) in the forests of
562 East Kalimantan. Biological Conservation 129, 566-578.
563 Mathewson, P.D., Spehar, S.N., Meijaard, E., Nardiyono, Purnomo, Sasmirul, A.,
564 Sudiyanto, Oman, Sulhnudin, Jasary, Jumali, Marshall, A.J., 2008. Evaluating
565 orangutan census techniques using nest decay rates: implications for population
566 estimates. Ecological Applications 18, 208-221.
567 McCullagh, P., Nelder, J.A., 1989. Generalized Linear Models. Chapman and Hall/CRC,
568 London.
569 Meijaard, E., 1997. A survey of some forested areas in South and Central Tapanuli, North
570 Sumatra; new chances for orang utan conservation. The International MOF
571 Tropenbos-Kalimantan Project and The Golden Ark Foundation, Bogor.
572 Meijaard, E., Albar, G., Nardiyono, Rayadin, Y., Ancrenaz, M., Spehar, S., 2010a.
573 Unexpected ecological resilience in Bornean orangutans and implications for pulp
574 and paper plantation management. PLOS ONE 5, e12813.
575 Meijaard, E., Mengersen, K., Buchori, D., Nurcahyo, A., Ancrenaz, M., Wich, S.,
576 Atmoko, S.S.U., Tjiu, A., Prasetyo, D., Nardiyono, Hadiprakarsa, Y., Christy, L.,
577 Wells, J., Albar, G., Marshall, A.J., 2011. Why don't we ask? A complementary
578 method for assessing the status of great apes. PLOS ONE 6, e18008.
579 Meijaard, E., Sheil, D., Nasi, R., Augeri, D., Rosenbaum, B., Iskandar, D., Setyawati, T.,
580 Lammertink, M., Rachmatika, I., Wong, A., Soehartono, T., Stanley, S., O'Brien, T.,
581 2005. Life after logging: reconciling wildlife conservation and production forestry in
582 Indonesian Borneo. Center for International Forestry Research, i-xxii, 1-345.
583 Meijaard, E., Welsh, A., Ancrenaz, M., Wich, S., Nijman, V., Marshall, A.J., 2010b.
584 Declining orangutan encounter rates from Wallace to the present suggest the species
585 was once more abundant. PLOS ONE 5, e12042.
586 Nater, A., Nietlisbach, P., Arora, N., van Schaik, C.P., van Noordwijk, M.A., Willems,
587 E.P., Singleton, I., Wich, S.A., Goossens, B., Warren, K.S., Verschoor, E.J.,
588 Perwitasari-Farajallah, D., Pamungkas, J., Krützen, M., 2011. Sex-biased dispersal
589 and volcanic activities shaped phylogeographic patterns of extant orangutans (genus:
590 *Pongo*). Molecular Biology and Evolution. 28, 2275–2288.
591 Peres, C.A., 1997. Effects of habitat quality and hunting pressure on arboreal folivore
592 densities in neotropical forests: A case study of howler monkeys (*Alouatta* spp.).
593 Folia Primatologica 68, 199-222.
594 Reinartz, G., Isia, I., Ngamankosi, M., Wema, L., 2006. Effects of forest type and human
595 presence on bonobo (*Pan paniscus*) density in the Salonga National Park.
596 International Journal of Primatology 27, 603-634.

Remis, M.J., Kpanou, J.-B., 2011. Primate and ungulate abundance in response to multi-use zoning and human extractive activities in a Central African Reserve. African Journal of Ecology 49, 70-80.
R Development Core Team: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, in Vienna, Austria. ISBN 3-900051-07-0, <http://www.R-project.org>.
Rijksen, H.D., Meijaard, E., 1999. Our vanishing relative: The status of wild orang-utans at the close of the twentieth century. Tropenbos Publications, Wageningen.
Şekercioglu, Ç.H., Ehrlich, P.R., Daily, G.C., Aygen, D., Goehring, D., Sandí, R.F., 2002. Disappearance of insectivorous birds from tropical forest fragments. Proceedings of the National Academy of Sciences 99, 263-267.
Singleton, I., Knott, C.D., Morrogh-Bernard, H.C., Wich, S.A., van Schaik, C.P., 2009. Ranging behavior of orangutan females and social organization, In Orangutans: Geographic variation n behavioral ecology and conservation. eds S.A. Wich, S.S. Utami Atmoko, T. Mitra Setia, C.P.v. Schaik, 205-213. Oxford Univ Press, New York.
Turner, I.M., 1996. Species loss in fragments of tropical rain forest: A review of the evidence. Journal of Applied Ecology 33, 200-209.
van Schaik, C.P., 2009. Geographic variation in the behavior of wild great apes: is it really cultural?, In The question of animal culture. eds K.N. Laland, B.F. Galef, pp. 70-98. Harvard Univ Press, Cambridge, MA.
van Schaik, C.P., Azwar, Priatna, D., 1995. Population estimates and habitat preferences of orang-utans based on line transects of nests, In The neglected ape. eds R.D. Nadler, B.F.M. Galdikas, L.K. Sheeran, N. Rosen, pp. 109-116. Plenum Press, New York.
Walsh, P.D., Abernethy, K.A., Bermejo, M., Beyers, R., De Wachter, P., Akou, M.E., Huijbregts, B., Mambounga, D.I., Toham, A.K., Kilbourn, A.M., Lahm, S.A., Latour, S., Maisels, F., Mbina, C., Mihindou, Y., Obiang, S.N., Effa, E.N., Starkey, M.P., Telfer, P., Thibault, M., Tutin, C.E.G., White, L.J.T., Wilkie, D.S., 2003. Catastrophic ape decline in western equatorial Africa. Nature 422, 611-614.
Walsh, P.D., Biek, R., Real, L.A., 2005. Wave-like spread of Ebola Zaire. PLoS Biology 3, 1946-1953.
Wich, S., Buij, R., van Schaik, C., 2004. Determinants of orangutan density in the dryland forests of the Leuser Ecosystem. Primates 45, 177-182.
Wich, S.A., Meijaard, E., Marshall, A.J., Husson, S., Ancrenaz, M., Lacy, R.C., van Schaik, C.P., Sugardjito, J., Simorangkir, T., Traylor-Holzer, K., Doughty, M., Supriatna, J., Dennis, R., Gumal, M., Knott, C.D., Singleton, I., 2008. Distribution and conservation status of the orang-utan (*Pongo* spp.) on Borneo and Sumatra: how many remain? Oryx, 329-339.
Wich, S.A., Singleton, I., Utami-Atmoko, S.S., Geurts, M.L., Rijksen, H.D., van Schaik, C.P., 2003. The status of the Sumatran orang-utan Pongo abelii: an update. Oryx 37, 49-54.

Supplementary Information S1

Identification of Covariates

Initially we identified eight covariates belonging to the four broad topography classes, vegetation, human impact and climate (Table S1.1). We selected these variables to well represent the environmental conditions of orang-utan habitat in Batang Toru. Although data stem from a range of years there are no indications that this might have influenced results.

Table S1.1: List of covariates

ID	Class	Covariate	Dataset description	Extraction
1	Topography	Elevation	DEM from SRTM; degree tile, 90m resolution SRTM_ffB03_p128r059 Downloaded from GLCF http:// http://glcf.umiacs.umd.edu/	Mean altitude in circle around midpoint of each transects with radius of half the transect length
2		Slope	Generated from degree tile, 90m resolution SRTM_ffB03_p128r059 http://www.glcf.org	Mean slope in circle around midpoint of each transects with radius of half the transect length
3	Vegetation	Forest type	Landsat 7 ETM+ classification (6 classes: 1-road; 2-cleared areas; 3-primary forest; 4-clouds; 5-logged forest; 6-mix of primary and logged forest) using 'random forest' package in R http:// www.glcf.org (image from 2004). Training database created by SW based on extensive field knowledge of the area.	Proportion of primary forest in circle around midpoint of each transects with radius of half the transect length
4		Above ground carbon	Based on 2005-2006 MODIS images. Provided by Woods Hole Research Center (for methods see: http://www.whrc.org/mapping/pantropical/modis.html) and Baccini et al in review.	Mean above ground carbon in circle around midpoint of each transects with radius of half the transect length
5	Human Impact	Hunting	Based on interview survey in neighboring villages, calculated as the number of people admitting to hunt orang-utans divided by the number of respondents (Usher et al. in prep. Available upon request)	Mean proportion of hunters in neighboring villages in circle with radius of 20km around each transect
6		Distance to forest edge	Forest cover layer generated in 2009 from 2004 Landsat 7 ETM + image	Distance of transect midpoint to forest edge
7	Climate	Mean annual rainfall	Extracted from Bioclim dataset, variable 12 http://www.worldclim.org	Mean annual rainfall in circle around midpoint of each transects with radius of half the transect length

8		Variation in annual rainfall	Extracted from Bioclim dataset, variable 15 (Coefficient of variation) http://www.worldclim.org	Mean coefficient of variation in circle around midpoint of each transects with radius of half the transect length

Selection of Covariates

Multicollinearity between predictor variables causes considerable problems in model fitting and interpretation of results. We therefore evaluated the degree of multicollinearity between the identified covariates by conducting correlation, principal component (PCA) and factor analyses (FA).

The Spearman correlation between all predictor variables showed a very high degree of correlation between several predictor variables (Table S1.2, Fig. S1.1).

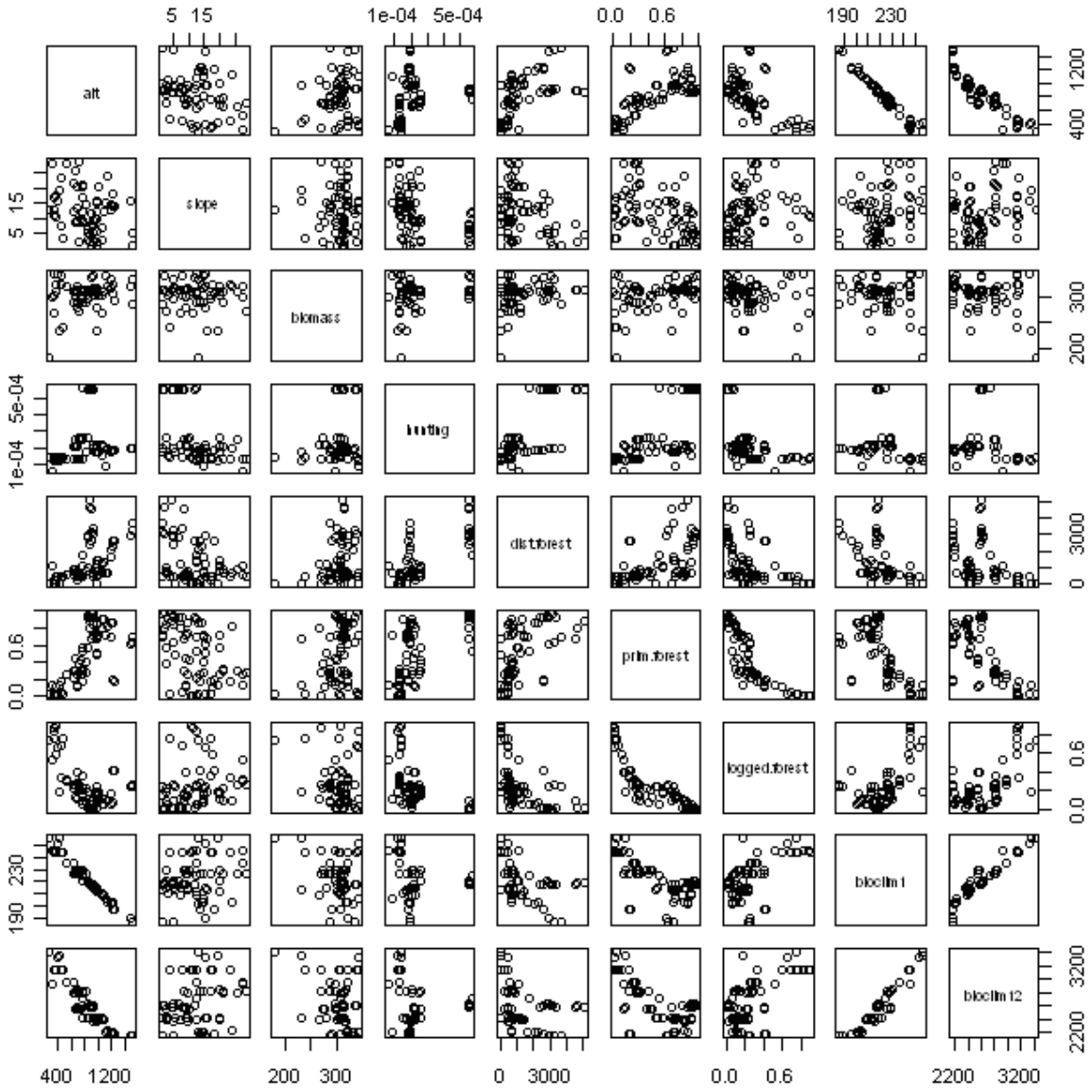
Table S.1.2: Results of spearman correlations between all pairs of predictor variables. The variables selected for the analysis are highlighted.

	alt	slope	biomass	hunting	dist.forest	prim.forest	logged.forest	bioclim1	bioclim12
alt	1.000	-0.206	0.376	0.026	0.263	0.504	-0.380	-0.951	-0.891
slope	-0.206	1.000	-0.011	-0.137	-0.114	-0.296	0.363	0.166	0.170
biomass	0.376	-0.011	1.000	0.283	0.362	0.644	-0.527	-0.382	-0.303
hunting	0.026	-0.137	0.283	1.000	0.320	0.386	-0.437	-0.025	0.110
dist.forest	0.263	-0.114	0.362	0.320	1.000	0.474	-0.452	-0.280	-0.129
prim.forest	0.504	-0.296	0.644	0.386	0.474	1.000	-0.870	-0.496	-0.384
logged.fores	-0.380	0.363	-0.527	-0.437	-0.452	-0.870	1.000	0.369	0.229
bioclim1	-0.951	0.166	-0.382	-0.025	-0.280	-0.496	0.369	1.000	0.926
bioclim12	-0.891	0.170	-0.303	0.110	-0.129	-0.384	0.229	0.926	1.000

We therefore tried to reduce the number of the nine predictor variables by conducting PCA and FA. However, both analyses did not considerably reduce the number of predictor variables. We therefore decided to conduct the analyses with a reduced set of predictor variables that still represented the ecological conditions and human pressure in

the area, however, which were not highly correlated with each other. These were ‘alt’, ‘slope’, ‘hunting’, ‘dist.forest’ and ‘prim.forest’.

Fig. S1.1 Pairwise plots of predictor variables



The variance inflation factors of the different variables Table S.1.3 were all below five, which is often suggested to be used as a threshold value indicating high multicollinearity.

Alt	Slope	Hunting	dist.forest	ht_3	ac_term
3.654681	1.496656	4.98177	3.757964	4.89579	1.249315

Table S1.3: Variance inflation factors for the different predictor variables derived from the model without squared terms and interactions.

Modeling

The average of model residuals weighted by the inverse distance (d_{ij}) to the focal transect is included as additional predictor into the model. To account for spatial autocorrelation, we first determined the residuals from the full model. Then, separately for each data point, we averaged the residuals of all other data points, with each residual's weight being a function of its distance to that data point. The weight followed a normal distribution (with a mean of zero), and we optimized the standard deviation of this distribution by minimizing the AIC of the full model with the derived autocorrelation term included in addition to the hunting pressure variable.

$$a_i = \sum_{j \neq i} \frac{obs_j - pred_j}{d_{ij}}$$

Last, we expected the variables altitude and hunting to influence orang-utan density in a nonlinear rather than linear way. We therefore included for these variables squared terms in the model. Also we considered hunting to interact with altitude. Thus, the model expression becomes

$$y_i = \exp(\ln(2 \times ESW \times l) + \alpha + \sum_{j=1}^{j=5} \beta_j x_{ij} + \sum_{k=1}^{k=2} \chi_k x_{ik}^{\ 2} + \delta x_{ij} x_{ij \neq k} + \gamma a_i + \varepsilon)$$

where y_i is the number of nests observed on transect *i*, α is the intercept of the linear predictor and ß$_j$ are the parameters for the linear predictors *j* with values x_{ij} at the sampling locations. χ_k are the parameters for the squared terms in the model, δ is the

parameter for the interaction between two predictors. γ is the parameter for the autocorrelation term a at transect location I and ε is the negative binomial error function. (*ln(2xESWxl)* is the offset term with l as the transect length and ESW as the effective strip width (Buckland et al. 2001, Hedley et al. 2004). *ESW* we estimated at 18.048 m using DISTANCE 6.0. We used a truncation distance of 40m, which reduced the total number of nests included into the analysis by 12 nests from 602 to 590.

Model diagnostics

We checked various diagnostics of model validity and stability (Cook's distance, dfbetas, dffits, leverage and variance inflation factors; distribution of residuals, residuals plotted against predicted values) and none of these indicated obvious influential cases or outliers, nor obvious deviations from the assumptions of normality and homogeneity of residuals (Quinn & Keough 2002, Field 2005).

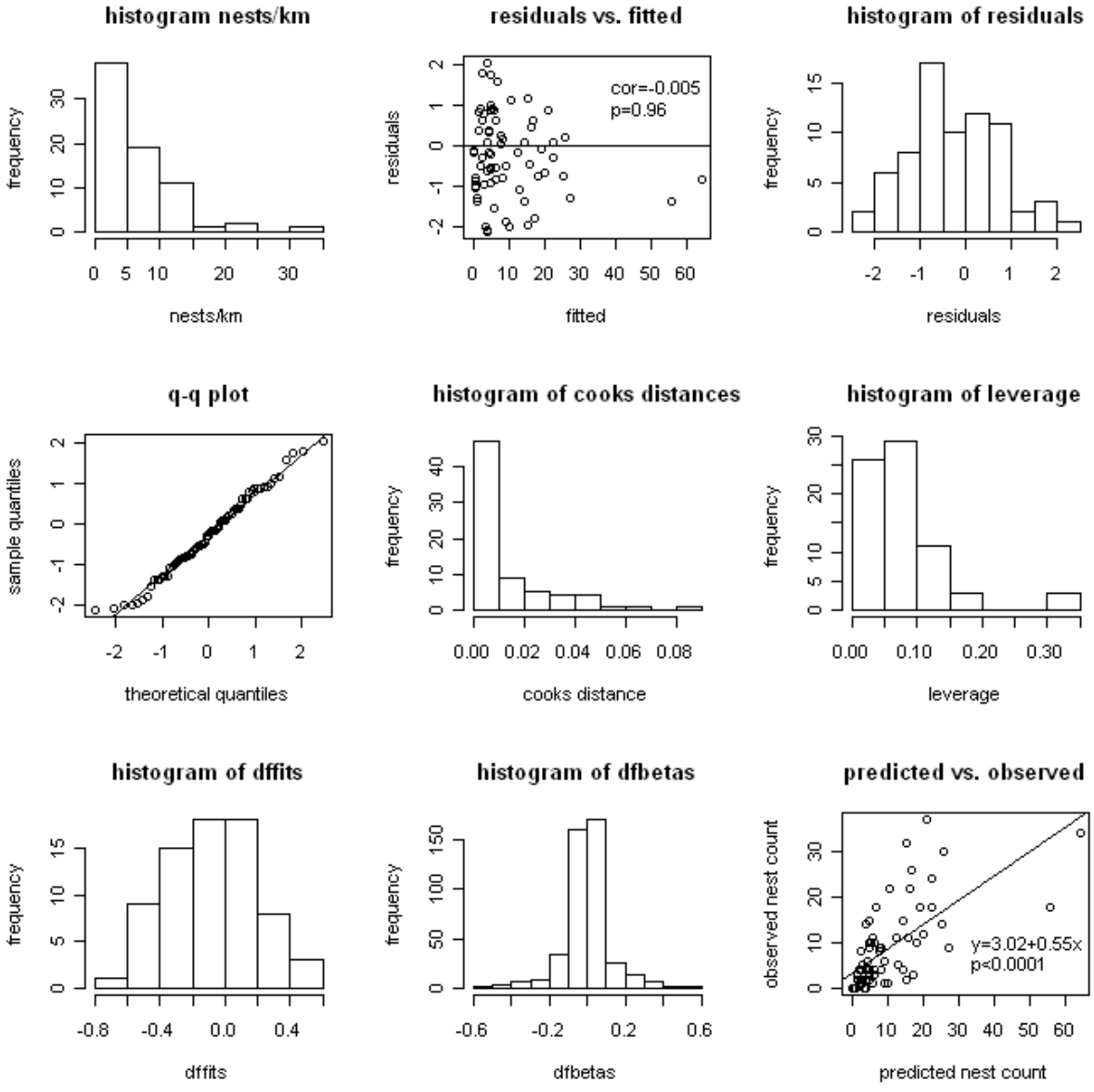


Fig. S1.2. Plots for model diagnostics

Nest decay

We estimated mean nest decay time by using a slightly modified approach of Laing et al. 2003. For each nest that did not completely decay during the study period we extracted from the repeat visits the number of days between the first observation of the nest and the last visit. For those nests that did decay during the study period we extracted the number of days between the first observation of the nest and the first visit, after the nest had decayed and in addition also the number of days between the first observation of the nest and the last visit before the nest had decayed.

We then maximized nest survival probability for surviving nests and maximized nest decay probability for nests that had decayed, by taking the difference in survival probability for the visit before and after decay. For nest survival probability we used the logistic model with

$$p_i(t) = \frac{(1+\exp(-(\alpha)))}{(1+\exp(-(\alpha+\beta*t)))} \ ,$$

p_i is the survival of nest *i* at time *t* after construction. The term (1+exp(-(α))) in the numerator ensures that p_i (0) =1.

We estimated parameters using the 'optim' function in R (R Development Core Team (2010). We then estimated mean decay time by summing the product of daily decay time and nest age over 2000 days. 95% confidence limits, we then estimated by bootstrapping our data 999 times, repeating the mean decay time estimation and took then from the ordered estimates, including the estimate for the original data the 25^{th} and 975^{th} value as lower and upper confidence limit.

Spatial predictions

The autocorrelation term we interpolated non-parametrically across the survey area by calculating for each grid cell an inverse distance weighted average of the autocorrelation term values at all sampled locations. To get confidence intervals for the estimated orang-utan density we ran 1,000 parametric bootstraps. For each bootstrap, we sampled a prediction per model and cell and then averaged them, weighted by the models' Akaike weights. We then determined the lower and upper 95% confidence limits per cell (i.e., per

116 km^2) using the percentile method (Manly 1997) and also the mean of the bootstraps per
117 cell.
118
119
120 **References**

121 Baccini, A., Goetz, S.J., Walker, W., Laporte, N.T., Sun, M., Sulla-Menashe, D., Hackler,
122 J., Beck, P., Dubayah, R., Friedl, M.A., Samanta, S., & Houghton, R.A. (in review)
123 Estimated CO2 emissions from tropical deforestation improved by carbon density maps.
124 Nature Climate Change.
125
126 Field, A. 2005. Discovering Statistics using SPSS. Sage Publications. London.
127
128 Manly, B.F.J. (1997) Randomization, Bootstrap, and Monte Carlo Methods in Biology,
129 2^{nd} edn. London: Chapmann & Hall.
130 Laing, S.E., Buckland, S.T., Burns, R.W., Lambie, D., Amphlett, A., 2003. Dung and
131 nest surveys: estimating decay rates. Journal of Applied Ecology 40, 1102-1111.
132
133 Quinn, GP & Keough, MJ. 2002. Experimental Designs and Data Analysis for Biologists.
134 Cambridge University Press. Cambridge.
135
136 R Development Core Team. 2010. R: A language and environment for statistical
137 computing. R Foundation for Statistical Computing, Vienna, Austria.

138